

Orientation and Response of *Tegula funebris* to Tidal Current and Turbulence

(Mollusca : Gastropoda)

BY

J. ALAN OVERHOLSER

Hopkins Marine Station of Stanford University,
Pacific Grove, California

(4 Text figures)

Tegula funebris (A. ADAMS, 1854) is a creature of the intertidal zone, and subject to the currents and turbulence caused by the incoming and outgoing waves. Because of the prevalence of these factors in its life, it seemed desirable to test the snail's behavioural response to them.

METHODS

A. Current: Two types of experiments were performed. (1) Individual *Tegula* were placed in a glass tube 76 cm long with an internal diameter of 2.15 cm, then subjected to a given current of sea water. Flow was uniform (flow characteristics were checked by the occasional addition of a little milk to the incoming water). Current was about 260 cm per minute; slope and light were controlled. Orientation of the snails was checked immediately before the current was started, and one minute after. (2) A number of *Tegula* was placed in a 2-liter Erlenmeyer flask half full of sea water, which then was placed on a magnetic stirrer. This produced a steady, uniform, horizontal current of about 450 cm per minute. This method introduces a vertical freedom of motion. As in all cases presented in this paper, day experiments were conducted in diffuse room light, night experiments in red light — 10 watt ruby bulb two feet away (shadow reaction tests showed the snails to be insensitive to this light).

Results: In the horizontal tube, with $N=255$, 64.4% went against the current, 32.1% went with it, and 3.5% sideways. No diurnal or tidal difference was found (all snails were freshly collected; snails were placed in the tube five minutes before starting the experiment). Previous orientation did have an effect: Of those originally oriented away from the current 61% turned into it; only 19% of those oriented into it turned away (Figures 1a, 1b).

Thus the snails were much more likely to go into the current than away from it.

In the magnetic mixer experiments, with $N=140$, 72% were oriented into the current after 30 minutes; only 14% were oriented away. The other 14% were either grouped, moving up the flask, oriented sideways, or not moving at all. Therefore, of those moving with respect to flow, 84% were moving against the current. Heating effects of the stirrer limited tests to about one hour — no more than a 3.5°C rise was allowed. One experiment was run for more than one hour, temperature being kept constant by running sea water. Figure 2 shows that the snails tend increasingly to go with the current after the first $3\frac{1}{2}$ hours. This may be the result of fatigue.

Current also has an effect on vertical distribution. For measuring this, the flasks were divided into three zones: A - the bottom quarter; B - the middle two quarters; C - the top quarter. Current tends to keep snails down, while controls go up (see Figures 3a, 3b). The only exception was the group, with control, run at sunrise. Other than this, no diurnal effect was noticed.

B. Turbulence: Two types of experiments were run. (1) Air was bubbled rather violently into 2-liter Erlenmeyer flasks full of sea water, containing a number of *Tegula* (usually 15). The amount of air entering was about 15 liters per minute. As in A (1) above, the flasks were divided into vertical zones A, B, and C. (2) This consisted of taking qualitative observations on the behavior and position of about 200 *Tegula* in an aquarium before and after heavy turbulence was produced with air. **Results:** In the flasks *Tegula* clusters very heavily around the air nozzle (at the bottom) by day; by night they cluster in the neck in the foam. Again, the controls

go up (Figures 4a, 4b). In aquaria turbulence produces great activity, and the snails tend to become randomly dispersed (at all other times they tend to clump: up at night, down at day). This result is more marked if the water level has been raised or lowered over a number of days. At sunrise and sunset there was greater activity, also.

Two preliminary experiments attempted to combine the effects of turbulence and current — this being a more natural field condition. (1) A small motor-driven propeller in an aquarium was pointed at a rock with *Tegula* on it. The orientation and position of each *Tegula* being noted, the propeller was run for one minute; the velocity of water approximated a medium-sized surge in the ocean on a quiet day. Orientation and position were again noted, both immediately and five minutes later. The results were consistent: the snails clamp hard, slowly orienting into the current. After it is stopped they rapidly move off, stopping when they reach a niche or crevice. (2) A *Tegula* was squirted with sea water direct from a tube; the stream had a velocity of 30m/minute. Results were again consistent: the snail clamps, leaves quickly when squirting ceases. The snail tends to go forward if squirted from behind, away if squirted from the front or side.

DISCUSSION

There is evidence that *Tegula* found the glass tube a "difficult" surface — probably due to its strong curvature

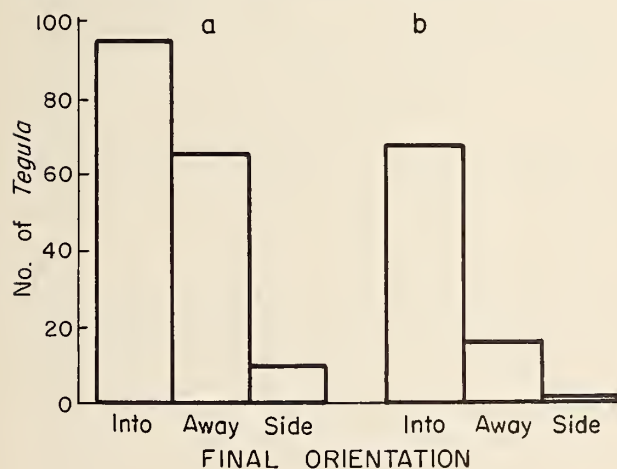


Figure 1: Orientation of *Tegula funebralis* with respect to current direction in a horizontal tube. Current of 260 centimeters per minute.
a - Original orientation away from current
b - Original orientation into current

(they would seldom encounter such a concave surface in nature). Many snails were washed off, even in weak currents; also, many of those oriented away made attempts to turn, but apparently could not (Note, in Figures 1a and 1b, that 10 of the 11 snails with a sideways final orientation were originally oriented away).

After a short while the behavior tended to become random (hence I used one minute as my marking point).

A possible source of error in the flask experiments was the magnetic stirrer: many snails were struck by it (whereupon they would promptly turn away), and since it was always spinning in the same direction.

In the bubbling flask experiments, there is evidence that air, and not turbulence, caused the observed effects. The snails always clustered around the air, whether down or up; evidently light caused the diurnal difference (KOSIN, 1964). If air bubbles were not present, a more intense light than that employed is needed to make them move down. HOLZ (1963) found that snails deprived of oxygen would revive faster in air than in water (even when heavily oxygenated), provided they are damp. Further, SNYDER (1964) found that respiration was greater at periods of low tide, while there was a lactic acid buildup at times of high tide: thus the presence of free air does seem to favor the respiratory activities of *Tegula funebralis*.

The question arises as to what sense organs are important in the current and turbulence behaviour of *Tegula funebralis*. Four large snails were deprived of epipodial tentacles and run in the magnetic stirrer flask: The results, though inconclusive, indicated a possible importance of these organs. Removal of head tentacles was not tried, but should be. Another possibility is the presence of some receptor sensitive to pressure applied to the shell. A suspended empty *Tegula* shell (aperture plugged with plasticene) which is free to turn will always orient forward when placed into a current, indicating less resistance; there is apparently a "resistance differential" for different orientations of the shell to oncoming current.

CONCLUSIONS

Tegula funebralis is activated when subjected to current and/or air turbulence; this behavior agrees with CLOUDSLEY-THOMPSON's remark (1961, p. 45) that many sea-shore animals are activated by waves. Further, current causes *Tegula* to orient into the flow, and also keeps them down near the bottom; if the current is sufficiently strong, however, they will often turn and head for shelter at the first respite. Preliminary tests in a vertical tube (250 cm/minute flow) indicate that snails tend to

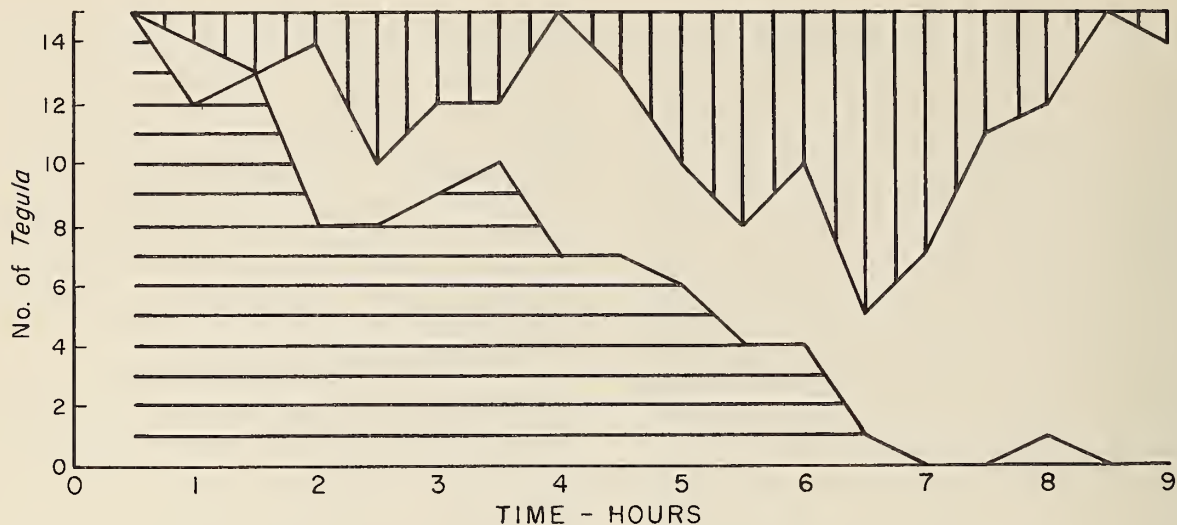


Figure 2: Change in the current orientation of *Tegula funebralis* with respect to time. Current of 450 centimeters per minute.
Horizontal lines = into current
Clear = away from current
Vertical lines = other orientation

go down *regardless of current direction*: evidently current stimulation, and not direction, causes *Tegula* to go down. It was shown that *Tegula* change their orientation to current after a few hours: this may be a set pattern of response, or perhaps the snails became fatigued. Gradation of current needs to be tried in all these cases. Finally, there is a definite response to air jets: the snails would clump in regions of greatest turbulence. This turbulence seemed to enhance the effect of light (the snails going down in light, up in dark). It is possible, however, that these results were due to the entering *air* rather than to the turbulence: further tests are definitely necessary.

Hypotheses: Perhaps an advantage of *Tegula funebralis*'s orientation into the current is increased chemo-receptive ability, important in the detection of food and predators; also, wastes may be carried away. As MORTON (1960, p. 149) notes: "The forward-facing mantle cavity in prosobranchs becomes the centre of all those functions depending on the passage of a water current: respiration, olfaction, detection and removal of sediment, and in a few cases feeding as well."

My results tend to explain two occurrences noted in the field: (1) *Tegula* congregates in turbulent areas — tops of rocks at night, swirling areas during day. (2) *Tegula* frequently does not make a large net movement

away from an original low-tide position after a complete tidal cycle. The first, (1), is expected because of the bubbling flask results; (2) is perhaps explained by the reversal in orientation to current noted in the long magnetic stirrer experiment.

ACKNOWLEDGMENT

The author is happy to acknowledge the advice of Professor L. R. Blinks.

LITERATURE CITED

- CLOUDSLEY-THOMPSON, J. L.
1961. Rhythmic activity in animal physiology and behaviour. New York and London, Acad. Press; 236 pp.; 33 text figs.
- HOLZ, WALTER
1963. Unpublished class report. Hopkins Marine Station
- KOSIN, DOROTHEA F.
1964. Light responses of *Tegula funebralis*. *The Veliger* 6; Supplement: 46-50; 7 text figs.
- MORTON, J. E.
1958. Molluscs: An introduction to their form and functions. New York, Harper Bros. 232 pp.; 23 text figs.
- SNYDER, JANNA M.
1963. Diurnal and tidal rhythm in the oxygen consumption of the gastropod *Tegula funebralis*. Unpublished student report, Hopkins Marine Station of Stanford University.

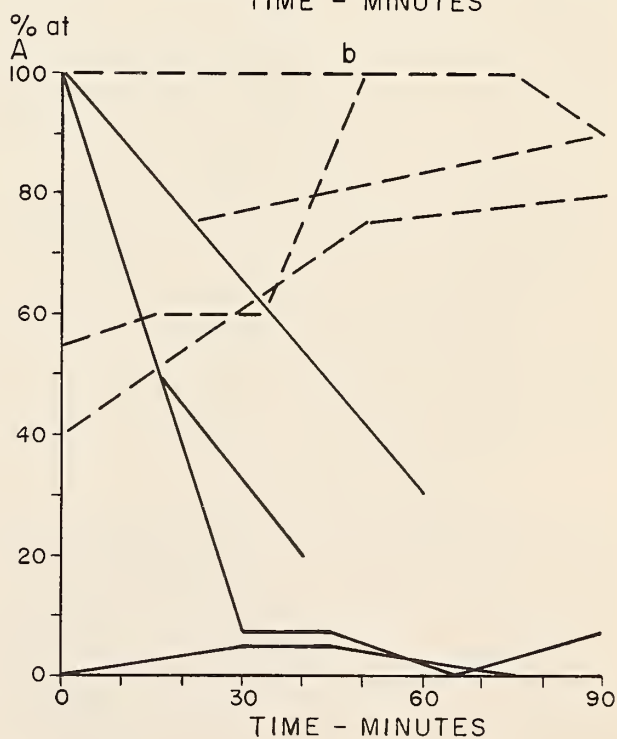
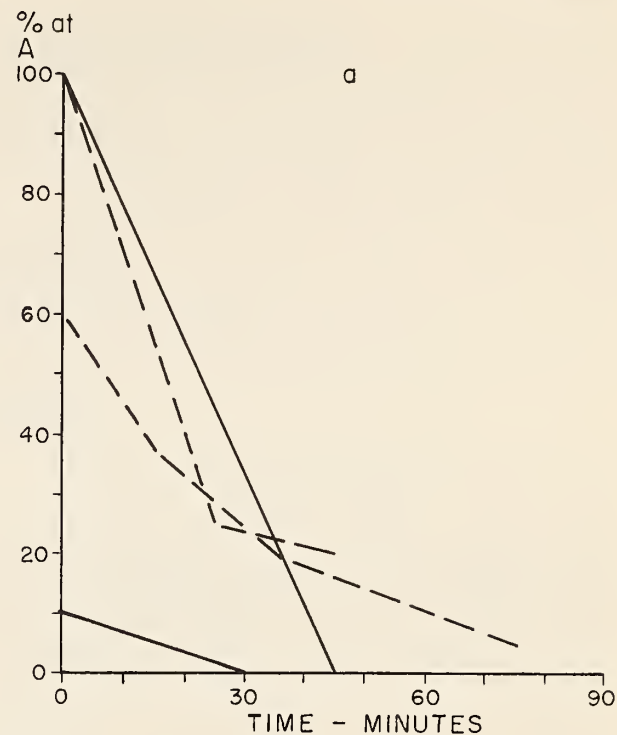
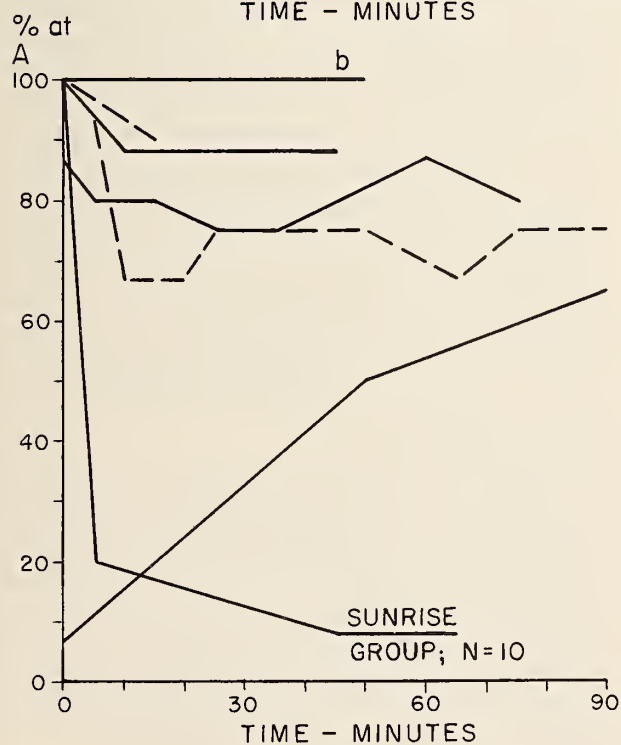
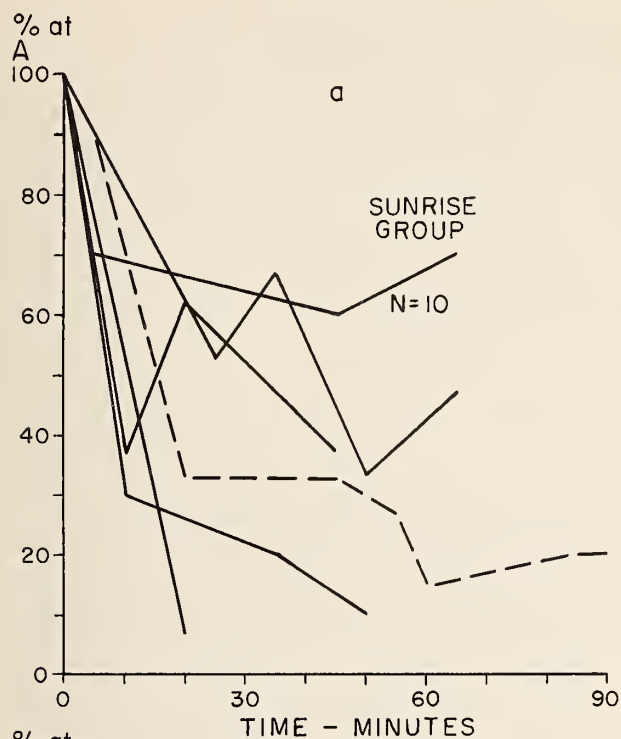


Figure 3: Current effect on vertical distribution of *Teglula funebris*. Current of 450 cm/min.

a. Controls

Solid line: Night - N = 48 (5 groups)

Broken line: Day - N = 25 (2 groups)

b. Tests

Solid line: Night - N = 65 (5 groups)

Broken line: Day - N = 25 (2 groups)

Figure 4: Turbulence effect on the vertical distribution of *Teglula funebris* (in flask)

a. Controls (quiet)

Solid line: Night - N = 40 (2 groups)

Broken line: Day - N = 35 (2 groups)

b. Tests (turbulent)

Solid line: Night - N = 70 (4 groups)

Broken line: Day - N = 69 (4 groups)